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Mar. 18, 1940

EVIDENCES OF RACIAL INFLUENCE IN A 25-YEAR TEST OF PONDEROSA PINE¹

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INTRODUCTION

The need for discrimination in collecting and importing forest-tree seed for planting was effectively pointed out by European foresters about 50 years ago, and some experimental plantings of seed from different sources were made in Europe at that time. About the opening of the present century, Cieslar (8)² and Engler (12) began intensive systematic investigations of the influence of seed origin on forest trees. The results showed definitely that when seed from the northern part or the higher altitudes of a tree's natural range in Europe was planted in the southern part or at the lower altitudes, the resulting trees grew less rapidly and developed less well than trees grown in the same localities from seed of local origin; and that if the offspring of parents adapted to the long growing seasons of low latitudes and low altitudes were planted in a more severe climate, they failed to survive or were badly deformed by frost injury.

To test the suitability of Scotch pine seed from various sources for planting in given parts of Europe, it was agreed at the 1906 meeting of the International Union of Forest Experiment Stations that the various countries within the range of the species should undertake an intensive cooperative experiment. Seed was collected from 12 widely scattered sources and planted in 1907 and 1908 in typical localities in Germany, Belgium, Netherlands, Sweden, Hungary, Austria, and Russia. In 1908 and 1909 a similar experiment with Scotch pine was started in Switzerland. Summarizations of the 20-year results of the international experiment and the Swiss experiment, by Wiedemann (35) and Burger (5), respectively, confirmed the conclusions derived from the earlier studies and added greatly to knowledge of the subject. They also indicated definite localities the seed of which is suitable for planting in other stated localities in Europe. These experiments and others having to do with the significance of seed origin have given rise to a wealth of literature, the extent of which is indicated by a bibliography compiled by Champion (7) containing 166 titles.

In American forestry literature, attention was called to the importance of seed origin by Zon (36) in 1913 and by Toumey (32) in 1914. Since then Pearson (24), Eckbo (11), Roeser (27), Bates (4), Austin (1), Baldwin (3), and other American foresters have published discussions of the subject. It has been common practice in

¹ Submitted for publication July 20, 1939.

² Italic numbers in parentheses refer to Literature Cited, p. 886.

the United States to collect forest-tree seed wherever it happened to be abundant and easy to obtain, with little regard to suitability for the locality where trees were to be grown or to the growth characteristics, form, or resistance to frost and disease that the trees might inherit. Only recently has some slight attention been given to the subject by planting and seed-collecting agencies.

As early as 1911 Zon, then in charge of silvicultural research in the Forest Service, started progeny experiments patterned after those in Europe at several of the newly established forest experiment stations in the Western States. Of these experiments, in which several species were used, only a few with ponderosa pine (*Pinus ponderosa*) and one with Douglas fir (*Pseudotsuga taxifolia*) (17, 22) are still in progress and are now yielding results.

The experiment with ponderosa pine discussed in this paper³ is one of these early projects and is, therefore, practically contemporaneous with the afore-mentioned European experiments. Seedlings grown from seed collected in many widely separated localities within the natural range of ponderosa pine were planted on an area in northern Idaho. The first plantings were made in the fall of 1911. The observations reported here extended to 1935.

The purposes of the study were stated at the time of its initiation as follows: (1) To determine the suitability of ponderosa pine seed from different sources for planting in northern Idaho; (2) to ascertain heritable characteristics of growth, form, and hardiness, developed through adjustment of parents to local climates; and (3) to determine what limitations should be placed on the interchange of seed between localities of different climate.

Nothing was known of the pollinating parents as distinct from the cone-bearing parents, and no information was recorded as to individual characteristics of the latter. In practical artificial reforestation, however, in which seed must be collected on a large scale and the forester is not yet able to control or identify the source of pollen, this lack of knowledge of individual parent trees will not seriously affect the application of results. Knowledge of the adaptability of trees grown from seed introduced from different localities is in itself a considerable contribution to the improvement of reforestation practice.

The existence of climatic races of forest trees is most evident in species having wide distribution in latitude, longitude, and altitude. Shaw (29, p. 23) states that—

“the range of variation is somewhat proportionate to change of climate. * * * The western species of North America, for instance, are much more variable than the eastern species, while in Mexico, a tropical country with snow-capped mountains, the variation is greatest.”

Thus ponderosa pine is particularly appropriate for a study of racial influence, for it is probably the most widely distributed conifer of western North America and certainly occurs in as great a diversity of climates as any other. Its range, according to Sudworth (30) and Munns (22a), extends in latitude from 23° in Mexico to 51°30' in British Columbia, and in longitude from 98° in Nebraska to 124° in California.

³ It is desired to acknowledge contributions to this project by D. R. Brewster, who prepared the working plan and supervised the installations, J. A. Larsen and G. Kempff, who made early examinations and records, C. A. Wellner and G. M. Fisher, who made recent measurements, and the late L. G. Hornby, who gave valuable help and advice in organizing the current results.

Two broad forms of ponderosa pine have long been recognized by foresters and dendrologists (16, 28, 30⁴)—the *scopulorum* form, occurring mainly east of the Continental Divide, and the *ponderosa* form, occurring west of the Divide. Some authorities have recognized the *scopulorum* form as a variety and some have given it specific status. In the present study such division of the species was disregarded and progenies were classified solely on the basis of evidence produced by the study.

CLIMATIC DATA OF THE LOCALITIES OF SEED ORIGIN

The various localities in which the ponderosa pine seed used in this study was collected are shown in figure 1. The climatic regions indicated were delimited chiefly on the basis of data on precipitation types given by Ward (33). The boundaries of these regions as shown must be regarded as approximations only. The South Pacific region is the only one not represented by any of the seed used. Each seed-source locality has been designated by the name of the national forest that contains it. Of the three localities on the Bitterroot Forest, at altitudes of 4,000, 5,000, and 7,200 feet, each has been treated separately and further designated by its elevation. Weather Bureau records were obtained for the stations nearest to and most representative of the individual localities of seed origin. Table 1 locates each point where seed was collected and gives details of the Weather Bureau stations at which the records were taken, and the periods of years represented by the records.

Mean annual and mean monthly precipitation was determined for each locality. These data are shown graphically in figure 2. Precipitation and temperature records are given in detail in table 2. Because precipitation and temperature in any locality vary with altitude, it was necessary in a few instances to make some adjustment for the considerable differences in altitude between place of seed origin and the nearest weather station. The adjustments made to render the records representative of these seed-collection sites are explained in the footnotes to the table. Table 2 further contains precipitation-effectiveness indices, showing the balance between evaporation and precipitation; the larger the values, the better the net result in plant growth.

Large variations in several factors are conspicuous as between the different localities. The lowest average annual precipitation was 13.05 inches, for Ashley, and the highest was 51.48 inches, for Siskiyou; the lowest July-August precipitation was 0.36 inch, for Siskiyou, and the highest was 8.83 inches, for Santa Fe.

Annual mean temperature was lowest (33.5° F.) for Bitterroot 7,200 feet and highest (50°) for Siskiyou. For January, the coldest month in every locality, Custer had the lowest mean, 16.8°, and Siskiyou the highest, 35°. The highest and lowest temperatures, 114° and -57°, were recorded in the same locality, Custer. The most equable climate is that of Siskiyou, where the extremes were 108° and -2°.

⁴ Also a preliminary study (unpublished) of the western yellow pine made by H. M. Curran in 1905. In Forest Service files.

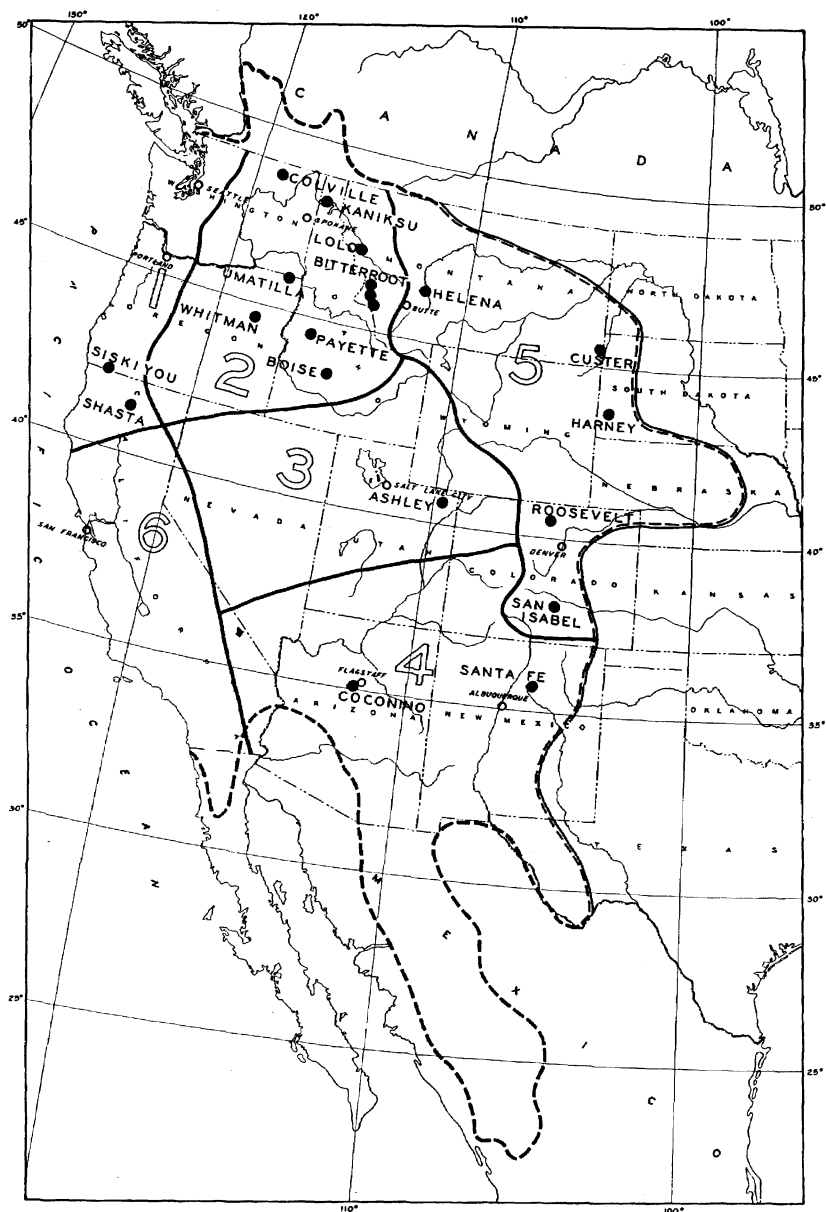


FIGURE 1.—Climatic regions of ponderosa pine range: (1) North Pacific; (2) north plateau; (3) central plateau; (4) south plateau; (5) east of Continental Divide; (6) South Pacific. The broken line shows the range of ponderosa pine according to Sudworth (30) and Munns (22a). Localities from which seed used in experiment was derived are indicated by black dots.

TABLE 1.—*Details of seed-collection points and corresponding weather-recording stations*

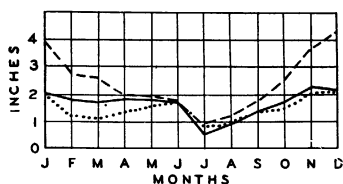
Location of seed-collection point ¹				Locus and extent of weather record				
Region and forest	Latitude	Longitude	Altitude	Locality	Altitude	Distance from seed source	Period of record	Length of record
	° ' "	° ' "	Feet		Feet	Miles		Years
North Pacific:								
Siskiyou.....	42 05	123 40	2,000	Waldo.....	1,650	5	1915-1935	16
Shasta ²	41 30	122 20	4,000	{McCloud.....	3,270	20	1911-1934	24
				{Mount Shasta.....	3,555	15	1888-1934	47
North plateau:								
Boise.....	43 30	115 00	5,500	Soldier Creek.....	5,755	20	1910-1935	26
Payette.....	44 30	116 00	5,000	McCall.....	5,025	20	1905-1935	22
Whitman.....	44 38	118 25	5,000	Austin.....	4,200	4	1916-1935	11
Umatilla.....	46 00	117 30	3,500	Wallowa.....	2,935	28	1915-1935	21
Colville.....	48 40	119 00	2,700	{Laurier.....	1,644	40	1910-1934	25
Kaniku.....	48 20	116 50	2,600	{Republic.....	2,628	10	1900-1934	29
				{Priest River Experiment Station.....	2,380	1	1912-1935	24
Lolo.....	47 10	114 50	3,000	Superior.....	2,975	3	1914-1934	19
Bitterroot.....	46 00	114 20	{4,000 5,000 7,200	{Como.....	3,750	5	1908-1921	14
South plateau:								
Coeonino.....	35 10	111 50	7,100	{Williams.....	6,750	20	1888-1934	35
				{Flagstaff.....	6,907	20	1888-1934	44
				{Fort Valley.....	7,300	25	1909-1934	22
				{Rociada.....	7,150	25	1904-1926	23
Santa Fe.....	35 40	105 30	8,000	{Gallinas Planting Station.....	7,500	15	1907-1930	24
				{Winsor's Ranch.....	8,000	25	1905-1935	40
East of Continental Divide:								
Helena.....	46 30	111 50	4,500	Helena.....	4,110	10	1880-1934	55
Custer.....	45 30	104 00	3,200	Camp Crook.....	3,103	10	1892-1935	42
Harney.....	43 40	103 30	5,000	{Deadwood.....	4,535	40	1917-1930	14
				{Custer.....	5,309	5	1911-1935	23
Roosevelt.....	40 30	105 40	8,000	{Morraine.....	7,775	10	1890-1916	26
San Isabel.....	38 00	105 00	8,000	{Estes Park.....	8,000	5	1909-1934	26
Central plateau:				{Goodpasture.....	6,120	10	1917-1926	8
Ashley.....	40 40	109 40	7,500	{Manila.....	6,225	20	1910-1934	25
				{Elkhorn-Ashley.....	6,657	10	1910-1934	25
				{Fruitland.....	7,000	50	1910-1929	20

¹ The localities are designated in the text by the names of the national forests containing them. The three localities on the Bitterroot National Forest are further designated by elevation. Seed was also collected on the Coeur d'Alene National Forest but proved to be valueless for this experiment since it comprised 2 distinct forms of ponderosa pine.

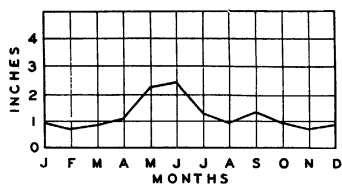
² All trees from this seed source were lost by freezing in 1924.

In considering the precipitation and temperature values in table 2 it should be borne in mind that these factors exert their influence on trees not independently but in combination, and that the altitude of the band on which ponderosa pine occurs increases from north to south, approximately at the rate of 350 feet for each degree of latitude.

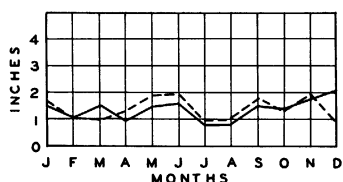
Because of the many factors involved for which no exact data on degree of influence are available, it is evident that only general conclusions can be reached as to correspondence between climate and regional form of ponderosa pine. Furthermore, the number of parent localities represented in this study is too small to make possible a close definition of the range of any regional form.



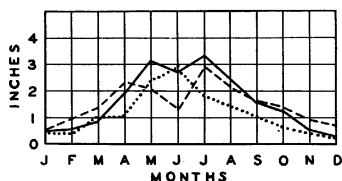
KANIKSU --- 28.70 in. annual
COLVILLE 17.28 in. annual
UMATILLA — 20.39 in. annual



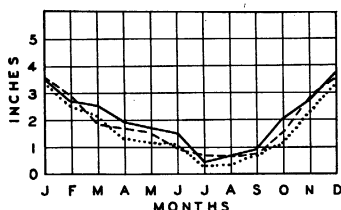
HELENA — 14.27 in. annual



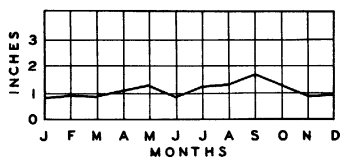
LOLO — 15.95 in. annual
BITTERROOT --- 16.53 in. annual



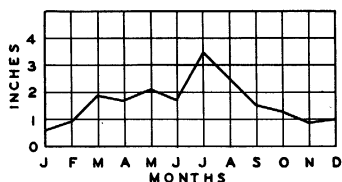
CUSTER 13.89 in. annual
HARNEY — 18.63 in. annual
ROOSEVELT --- 17.82 in. annual



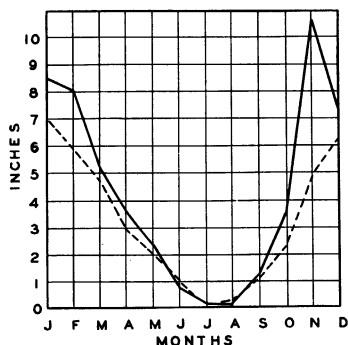
WHITMAN 19.48 in. annual
PAYETTE — 24.30 in. annual
BOISE --- 22.21 in. annual



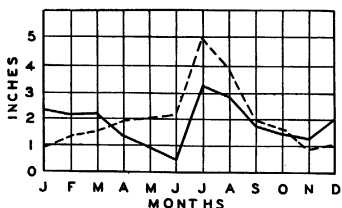
ASHLEY — 13.05 in. annual



SAN ISABEL — 19.80 in. annual



SISKIYOU — 51.48 in. annual
SHASTA --- 38.47 in. annual



COCONINO — 22.06 in. annual
SANTA FE --- 24.12 in. annual

FIGURE 2.—Precipitation types of localities of seed origin.

TABLE 2.—Summary of weather records for localities of seed origin

Region and forest.	Average precipitation ¹				Mini- mum annual precip- itation	Average temperature ²			Extremes of temperature		Average date of first 40° F. daily mean	Precip- itation- effective- ness indices ³	Aver- age frost- less season ⁴ Days	Latest frost on record ⁴	Earliest frost on record ⁴	
	Annual	April, May, and June	July and August	April- August, inclu- sive		Annual	April, May, and June	July and August	Highest	Lowest						
North Pacific:	Inches	Inches	Inches	Inches	Inches	° F.	° F.	° F.	° F.	° F.	° F.					
Siskiyou.....	51.48	6.49	0.36	6.85	36.79	50.0	54.1	66.6	108	-2	Feb. 20	164.1	159	June 11	Sept. 3	
Shasta.....	38.47	5.83	.42	6.25	21.33	47.0	51.3	63.7	106	-11	Mar. 20	138.0	108	July 6	Aug. 24	
North plateau:																
Boise.....	22.21	4.10	1.25	5.35	13.45	42.3	48.8	65.1	100	-26	Apr. 15	85.0	78	July 30	Aug. 1	
Payette.....	24.30	5.11	1.03	6.14	13.82	40.2	47.0	62.4	104	-46	Apr. 20	95.6	69	July 26	Aug. 4	
Whitman.....	19.48	3.41	.61	4.02	12.61	39.0	46.1	58.7	101	-40	do	79.5	110	June 30	Aug. 15	
Umatilla.....	20.39	5.44	1.49	6.93	10.60	43.3	50.3	63.7	106	-40	Apr. 1	65.4	88	July 14	Aug. 6	
Colville.....	17.28	4.56	1.75	6.31	9.81	43.6	51.7	63.7	109	-35	do	52.9	62	July 27	Aug. 13	
Kaniksu.....	28.70	5.52	1.87	7.39	16.02	43.3	50.8	63.2	102	-35	Apr. 5	104.9	103	July 1	Do.	
Lolo.....	15.95	4.06	1.57	5.63	7.61	44.9	52.1	66.0	104	-33	Mar. 25	46.5	127	June 8	Aug. 25	
Bitterroot:																
4,000 feet.....						44.2	51.4	64.0	103	-33	Apr. 1	45.4				
5,000 feet.....	16.53	5.05	1.95	7.00	13.58	41.0	48.2	60.8			Apr. 10					
7,200 feet.....						33.5	40.7	53.3			May 10					
South plateau:																
Cocoino.....	22.06	2.83	6.20	9.03	11.79	45.4	50.7	64.1	102	-33	Apr. 5	62.6	110	July 29	Aug. 15	
Santa Fe.....	24.12	6.04	8.83	14.87	14.84	42.9	48.1	59.4	92	-33	Apr. 15	59.0	116	July 21	Aug. 20	
East of Continental Divide:																
Helena.....	14.27	5.80	2.10	7.90	7.38	42.2	50.3	65.2	102	-43	Apr. 10	36.1	145	June 9	Aug. 25	
Custer.....	13.89	6.30	3.16	9.46	6.50	43.3	53.1	69.1	114	-57	do	28.5	120	June 28	Aug. 28	
Harney.....	18.63	7.61	5.80	13.41	9.27	41.9	49.4	64.1	100	-31	do	41.3	91	June 17	Aug. 25	
Roosevelt.....	17.82	5.68	4.90	10.58	11.08	41.4	46.6	59.8	98	-42	Apr. 25	48.1	91	July 20	Aug. 17	
San Isabel.....	19.80	5.54	5.97	11.51	13.35	41.7	48.6	62.3	96	-36	Apr. 20	52.7	85	July 10	Aug. 25	
Central plateau: Ashley.....	13.05	3.34	2.51	5.85	6.35	39.6	46.4	61.2	94	-36	Apr. 25	35.1				

¹ All the precipitation figures, except those for 4 localities, are exactly as shown by the basic weather-station data used. For the Whitman and Helena localities the weather-station records were increased 10 percent, and for the Umatilla locality they were increased 25 percent, to make them representative of the seed-collection points. This was done on the advice of the local forest officers, and by checking against precipitation maps of the Atlas of American Agriculture (25). For the Colville locality the local forest officer recommended use of the Laurier precipitation records as more representative than those of the more closely located Republic weather station. With these corrections, the figures approximate closely the precipitation of 16 of the localities of seed origin. The Ashley, San Isabel, Bitterroot 5,000 feet, and Bitterroot 7,200 feet seed-origin points are 843 to 3,450 feet higher than the local weather stations, and doubtless have somewhat greater precipitation than is shown here; but basic data are not available for correction.

² To make temperature figures of weather stations representative for seed-origin localities at greater altitudes, the customary reduction of 3.3° F. was made for every 1,000-foot difference in altitude.

³ Precipitation-effectiveness indices for weather stations, computed by Thornthwaite's (3) method for integrating the effect of evaporation and precipitation.

⁴ The frost figures are those of the weather stations, without adjustment. Except for the Umatilla, Bitterroot, Ashley, and Helena localities, it is believed that the frost conditions at the localities of seed origin are but slightly different from those at the weather stations.

EXPERIMENTAL AREA AND PLOTS

The experimental plantation is a part of the Priest River experimental forest of the Northern Rocky Mountain Forest and Range Experiment Station, located on the Kaniksu National Forest, in northern Idaho. It has an elevation of 2,380 feet. The climate is typical for the western white pine forest, with a mean annual precipitation of 28.70 inches, a moderately deep accumulation of snow, and a fairly heavy spring rainfall. July and August are characteristically hot and dry, with an average total of only 1.87 inches of rain and with prevailing low relative humidity, which frequently goes below 15 percent. The annual mean temperature is 43.3° F., and frost may occur in any month.

The Kaniksu Forest is mainly occupied by the typical mixed stands of the western white pine type, composed principally of western white pine (*Pinus monticola*), western larch (*Larix occidentalis*), Douglas fir, lowland white fir (*Abies grandis*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*). Dry south slopes within the type often contain some ponderosa pine in mixture with the less moisture loving of the above species.

The progeny plots are situated in a clearing near the outer edge of a bench otherwise occupied by a natural second-growth stand in which larch and Douglas fir predominate over western white pine. A southwest slope that rises from the edge of the bench close to the plots has a natural open cover of ponderosa pine, larch, and Douglas fir. The bench has the appearance of an old river terrace. Lapham and Youngs⁵ mapped the soil as Springdale sandy loam and described it as follows:

The surface soil of the Springdale sandy loam is a friable fine to medium sandy loam, containing a small amount of gravel * * *. This material extends to a depth of 1 to 2 feet, * * * and overlies a subsoil of loose sand and gravel. This gravel is largely granitic and may be glacial outwash. The substratum, [which is] at a considerable depth, consists of old-lake clays.

* * * The surface drainage is good and the subdrainage is generally excessive. The water-holding capacity is low due to thinness of the soil above the porous subsoil. This porous material also minimizes the upward movement of the capillary moisture. Altogether this is a droughty soil.

Small gravel pits were dug at three widely scattered points on the bench to a depth of 8 feet without exposing the clay substratum. The soil is very deficient in humus as a result of forest fires, which in about 1855 destroyed the virgin forest and some 40 years later destroyed a second-growth stand. A record made in 1917 stated that the soil retained moisture fairly well until about the middle of August, when it dried out to a moisture content of 3 or 4 percent of oven-dry weight at a depth of 12 inches, and then remained unchanged until the beginning of fall rains in September. Soil samples taken at a depth of 24 inches in the centers of all plots on August 31, 1936, had a moisture content ranging from 3 to 9 percent and averaging 4.7 percent. Recent soil-acidity tests made at three points on the planted area showed pH values ranging from 6.2 to 6.8. Rather too well drained for western white pine, the site of the plots appears from the growth rate and vigor of the planted trees to be well suited for ponderosa pine.

⁵ LAPHAM, M. H., and YOUNGS, F. O. SOIL SURVEY OF THE PRIEST RIVER FOREST EXPERIMENT STATION. 1925. [Unpublished manuscript.]

As site conditions are practically uniform on the cleared part of the bench, and as the progeny plots form a small, compact block only 200 by 260 feet in size, the plots may be said to have closely comparable growing conditions. Because the foot of a slope touches the northeast corner of the plantation, however, three plots (the Bitterroot 7,200 feet, the Lolo, and the Bitterroot 4,000 feet) might be assumed to have an advantage as to soil moisture. As the slope has a southwest exposure, however, and the short distance to the ridge top precludes retention of any great amount of water, the advantage if any is not marked. Actual tests showed the Lolo and Bitterroot, 4,000 feet, plots to have slightly less soil moisture than the average for all the plots.

Although the crown canopy on some of the plots has become dense enough to shade out low vegetation in spots, most of the ground surface is still covered with herbaceous and shrubby vegetation of vary-

Payette June 5, 1912	Coconino May 10, 1912		Santa Fe May 3, 1915	Lolo May 2, 1916	Bitterroot 7,200 feet May 29, 1917
Coeur d'Alene Oct. 6, 1911 (excluded)	Custer Oct. 6, 1911		Ashley May 13, 1915	Kaniksu May 2, 1916	Bitterroot 4,000 feet May 31, 1917
Helena Oct. 14, 1911	San Isabel Oct. 14, 1911	Roose- velt June 5, 1912	Bitterroot 5,000 feet May 13, 1915	Siskiyou May 3, 1916	Harney May 2, 1916
Shasta May 13, 1915 (excluded)	Uma- tilla Nov. 18, 1911	Whit- man May 13, 1916	Boise May 13, 1915	Colville May 13, 1915	Unknown Origin April 29, 1916 (excluded)

FIGURE 3.—Arrangement of progeny plots, and dates of first planting. The large plots are 50 by 50 feet and the small ones 25 by 50 feet.

ing density. The most abundant species are *Arctostaphylos uva-ursi*, composing 25 to 75 percent of the low vegetation, and *Calamagrostis rubescens*, composing 10 to 65 percent. Other characteristic species, in the order of their abundance, are *Fragaria glauca*, *Pentstemon* sp., *Achillea lanulosa*, *Symphoricarpos racemosus*, *Odostemon aquifolium* (syn. *Berberis aquifolium*), *Pteridium aquilinum pubescens*, and *Ceanothus velutinus*. All these species are typical of the drier sites in this locality.

The progeny trees representing each locality of seed origin were planted on 1 of the 22 plots shown in figure 3. On each of the 18 large plots, 50 feet square, 100 trees were planted, and on each of the 4 small ones, 25 by 50 feet, 50 trees were planted. Spacing of trees was exactly 5 by 5 feet.

The stock used in the first 8 plot installations, made in the fall of 1911 and the spring of 1912, and in 3 made in 1913, 1915, and 1916, was grown in Forest Service nurseries in various regions. For the 11 other installations, made in 1915, 1916, and 1917, stock was grown in a small nursery at the site of the experiment. The trees were planted

on the plots as 2- and 3-year-old transplants. The method was to dig an open hole, spread the roots around a mound of earth in the center, and firm the soil by hand.

For 3 to 5 years after each first installation, all trees that died were replaced with trees of the same lot that had been reserved in the nursery, in order to maintain closed-stand conditions.

Of the 22 progenies shown in figure 3, only 19 are treated in this report. All the trees on the Shasta plot were lost by freezing in 1924. Because its seed-source record is very questionable, the plot designated "Unknown origin" was omitted. The plot designated "Coeur d'Alene" has a mixture of two distinct forms of ponderosa pine and was therefore excluded also.

Every year from 1912 to 1919, the plots were examined and a record was made of the number of living and dead trees, the number of replacements, and the height of a representative 20 percent of the trees on each plot. Similar records including heights of all trees were made in 1927 (14). In 1935, measurements of height and diameter were made on all the trees, and also of internode lengths of the main stem for the years 1930-35. Records were made, also, of survival, vigor, dominance, and foliage characteristics.

FOLIAGE CHARACTERISTICS

The foliage of each progeny was classified as to number of needles per fascicle, length of needles, number of years needles were retained, general appearance of foliage, and internal structure of needles. In this connection it should be kept in mind that the progenies are about the same age, are situated close together on level ground practically uniform as to soil and moisture, and are uniformly exposed to sun and wind.

NUMBER OF NEEDLES IN FASCICLE

In discussing the pines, Shaw (29, p. 4) says:

The number of leaves in the fascicle is virtually constant in most species, the variations being too rare to be worthy of consideration. With some species, however, heteromerous fascicles are normal. The influences that cause this variation are not always apparent (*echinata*, etc.), but with *P. ponderosa*, *leophylla*, *sinensis*, and others, the number of leaves in the fascicle is, in some degree, dependent on climatic conditions, the smaller number occurring in colder regions.

The fascicles of *Pinus ponderosa*, Shaw states, consist prevaingly of three needles each, but range from two to five or more, the larger numbers occurring in the southern part of the tree's range.

In the progenies of this experiment the number of needles to the fascicle varied from two to three. To determine the proportions of two- and three-needle fascicles, an examination was made of the foliage of 20 trees on each of the progeny plots. On each of these trees 10 fascicles were examined on each of 5 branches selected at random from the lower half of the crown. On each branch, approximately equal numbers of fascicles were examined on each of the internodes having green needles. A separate record was kept for each tree. For each plot the average percentage of fascicles containing three needles was determined, as shown in table 3.

Comparison of progeny trees with native trees as to the proportion of three-needle fascicles was made by the use of specimen branches obtained from the parent localities. As the foliage in any locality

may vary greatly among individual trees according to age of tree, exposure, and character and moisture content of the soil, and on a single tree according to position in the crown, collectors were requested to select outer branches below the middle of the crown on the south sides of vigorous trees, 20 to 40 years old, growing in open stands on good sites. Thus an effort was made to obtain foliage specimens from the same general position in the crown and from the same kinds of trees as on the progeny plots. From 3 to 10 specimens, representing that number of trees, were obtained from each locality. On each branch 50 fascicles were examined, a total of 150 to 500 for each locality. The results are presented in table 3.

TABLE 3.—Percentage of fascicles containing three needles,¹ on progeny plots and in parent localities

Climatic region and locality of seed origin	Fascicles containing 3 needles		Group character
	Progeny plot	Parent locality	
	Percent	Percent	
North Pacific: Siskiyou.....	93	100	Typically 3-needed.
North plateau:			
Boise.....	95	99	
Payette.....	97	100	
Whitman.....	98	93	
Umatilla.....	98	100	
Colville.....	93	100	
Kaniksu.....	93	94	
Lolo.....	95	99	
Bitterroot:			
4,000 feet.....	97	95	
3,000 feet.....	94	98	
7,200 feet.....	95	99	
South plateau:			Typically 2-needed.
Coconino.....	94	97	
Santa Fe.....	92	96	
East of Continental Divide:			
Helena.....	69	88	
Custer.....	24	25	
Harney.....	24	7	
Roosevelt.....	11	22	
San Isabel.....	51	43	
Central plateau: Ashley.....	60	76	Intermediate.

¹ All fascicles not containing 3 needles contained 2.

In all cases, the findings for trees in a parent locality and those for the progeny derived from that locality were similar, indicating that number of needles to the fascicle is an inherited characteristic persisting at least through the first 22 to 26 years of the progeny's life. The evidence from the areas sampled shows that in general three-needle fascicles are characteristic of ponderosa pine in the north and south plateau regions and two-needle fascicles are characteristic east of the Continental Divide. The Helena locality, close to the Divide on the east, is an exception. The Ashley locality, in the central plateau region, tends to be intermediate.

LENGTH AND PERSISTENCE OF NEEDLES

With regard to variation in needle length, Shaw (29, p. 4) says:

Among conifers, the leaf of *Pinus* attains extraordinary length with great variation, * * * the maximum for each species being usually much more than twice the minimum. Climate is the predominating influence; for the shortest leaves occur on alpine and boreal species, the longest leaves on species in or near the tropics.

The length of the leaf is complicated by the peculiarities of individual trees and by pathological influences; as a general rule, however, the length of leaves is less or greater according to unfavorable or favorable conditions of temperature, moisture, soil and exposure. Therefore the dimensions of the leaf may be misleading. It can be said, however, that certain species always produce short leaves, others leaves of medium length, and others very long leaves.

Data on needle length were collected not only on progeny trees but also on trees in the parent localities. The method of selection was to pluck at random 10 or more fascicles from 1 branch on each of 3 trees, taking a proportionate number from each of the internodes. Measurements were made of 30 or more needle clusters for each progeny plot, and 50 for each parent locality. Average length was calculated for the shortest 10 and the longest 10 to obtain "principal range," and for the total number of fascicles.

TABLE 4.—*Length of needles on progeny plots and in parent localities*

Climatic region and locality of seed origin	Progeny plot		Parent locality		Group character
	Principal range	Average	Principal range	Average	
North Pacific: Siskiyou.....	<i>Inches</i> 4.8-6.6	<i>Inches</i> 5.9	<i>Inches</i> 4.9-7.6	<i>Inches</i> 6.4	Long.
North plateau:					
Boise.....	4.8-6.5	5.8	4.8-7.5	6.1	
Payette.....	4.4-6.8	5.6	4.4-6.6	5.7	
Whitman.....	4.2-6.9	5.9	4.8-6.7	5.9	
Umatilla.....	4.7-6.6	5.8	5.4-7.9	6.9	
Colville.....	4.7-5.8	5.4	5.1-6.6	5.7	
Kaniksu.....	4.7-6.2	5.6	5.0-7.1	6.0	
Lolo.....	5.8-6.8	6.3	5.1-7.1	6.1	
Bitterroot:					
4,000 feet.....	4.9-7.4	6.1	5.1-6.8	6.1	
5,000 feet.....	4.3-6.7	5.6	3.5-6.3	4.8	
7,200 feet.....	4.0-5.9	5.0	3.7-6.0	5.0	
South plateau:					Medium to long.
Coeur d'Alene.....	4.0-5.8	4.9	4.5-6.2	5.4	
Santa Fe.....	3.9-5.3	4.6	4.7-7.6	6.2	
East of Continental Divide:					
Helena.....	3.9-5.7	4.9	5.8-7.6	6.7	Short.
Custer.....	3.0-4.2	3.7	4.4-6.8	5.7	
Harney.....	2.7-3.9	3.4	3.2-5.3	4.3	
Roosevelt.....	2.9-4.7	3.8	3.2-4.8	4.1	
San Isabel.....	3.2-5.0	4.2	4.2-6.0	5.2	
Central plateau: Ashley.....	3.2-5.2	4.3	3.2-5.2	4.2	

It appears from the data in table 4 that characteristics as to needle length were hereditary in the progenies studied, at least for the first 22 to 26 years of their lives; that is, that for 20 years and more the progeny have for the most part fallen into the same general classifications of long, medium, and short needles as did the trees in the parent localities. The data show that the needles of trees of the North Pacific and north plateau regions are long, that those of the south plateau are medium to long, and that those of the central plateau and of the localities east of the Continental Divide are short. The Helena trees are again an exception, their needles being medium to long, more like those of localities west of the Divide.

Data on persistence, or the number of years needles remain green on the tree, were obtained for the progeny plots by recording for each of 5 branches on 20 trees per plot the number of internodes having green needles. Corresponding data for trees of the parent localities

were obtained by examining all the specimen branches collected in each locality. These data are presented in table 5.

TABLE 5.—Number of years needles persist on progeny plots and in parent localities

Climatic region and locality of seed origin	Progeny plot		Parent locality	
	Principal range	Mode ¹	Principal range	Mode ¹
	Years	Years	Years	Years
North Pacific: Siskiyou.....	2-4	3	2-3	3
North plateau:				
Boise.....	3-4	3	4-5	4
Payette.....	3-4	3	4-5	4
Whitman.....	3-4	3	² 4-6	² 5
Umatilla.....	3-4	3	5-6	6
Colville.....	3-4	4	4-5	5
Kaniksu.....	3-4	4	4-5	5
Lolo.....	3-4	3	4-5	5
Bitterroot:				
4,000 feet.....	3-4	4	4-5	4
5,000 feet.....	3-4	4	4-5	4
7,200 feet.....	3-4	3	4-5	4
South plateau:				
Coconino.....	3-4	3	² 4-7	² 6
Santa Fe.....	3-4	3	(³)	(³)
East of Continental Divide:				
Helena.....	3-4	3	4-5	5
Custer.....	3-4	4	4-6	5
Harney.....	3-4	4	3-4	4
Roosevelt.....	3-4	4	5-7	6
San Isabel.....	3-4	3	4-6	6
Central plateau: Ashley.....	3-4	3	6-9	8

¹ The value occurring in the greatest number of cases.

² Values estimated on basis of incomplete evidence.

³ Evidence available too incomplete to serve as basis for estimate.

Persistence is closely related to needle length. In general, where the growing season is short and rigorous, as at high altitudes, both shoots and needles are short. To compensate for this dual dimensional deficiency, needles must persist on more internodes than under more favorable conditions. Examples of high-altitude species having short needles persisting over a long period are *Pinus albicaulis* and *P. balfouriana*.

Needles persisted mainly 4 or 5 years in parent localities in the north plateau region, 6 years in the more severe Roosevelt and San Isabel localities, and 8 years in the rigorous Ashley locality; but needles on the progeny trees uniformly persisted only 3 or 4 years, regardless of origin. Thus it appears that, in ponderosa pine, needle persistence is not inherited, and that if the same area of leaf surface is maintained in the Priest River as, for example, in the Ashley environment this is done in some other way than by long retention of needles. The method of adjustment in this particular case is indicated by the fact that the length of the three internodes containing green needles on Ashley progeny trees averaged practically the same as the length of the eight internodes containing green needles on Ashley parent-locality trees.

It is interesting to note that in experimental plantations in Switzerland containing trees of different seed origin, Burger (5) and Nägeli (23) found needle persistence of Scotch pine and Norway spruce, respectively, to be uniform regardless of shorter or longer retention in different parent localities.

INTERNAL STRUCTURE OF NEEDLES

In order to ascertain what differences in needle structure exist among the progenies of this experiment, arrangement was made with J. H. Ramskill, professor of forestry in the University of Montana, to undertake cooperatively a microscopic study of the needles. Professor Ramskill was supplied with needles from each progeny plot and from each parent locality, collected according to methods of sampling already described. He made a great number of cross sections from these needles, studied 688 of them, and made photomicrographs of selected sections. Some of the structural characteristics found by Ramskill to be most consistent and most clearly heritable are here summarized.

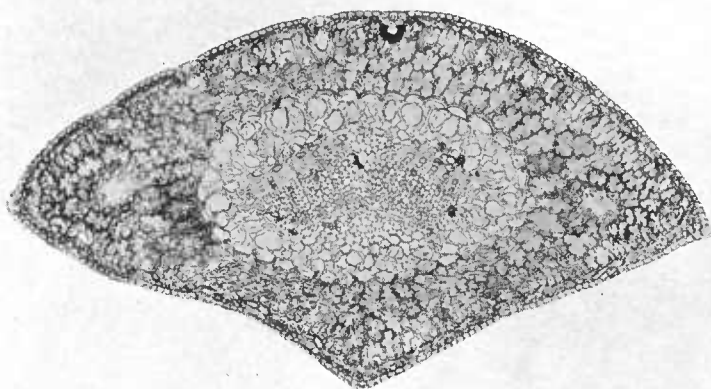
Leaf features in which plants are known to make protective adjustments in different habitats are thickness of hypoderm and character of stomatal chambers. The hypoderm in ponderosa pine is biform, having an outer row of cells (next to the epidermis) which is always thin-walled and an inner row or several inner rows of cells which may be thick-walled or thin-walled. In localities of severe climate, the inner rows may be many and composed solidly of thick-walled cells; in localities of moderate climate, they may be fewer in number and composed of thick-walled and thin-walled cells interspersed; in localities of mild climate there may be only one or two inner rows composed mainly of thin-walled cells, with a few interspersed thick-walled cells.

The observed extremes in these features are shown in plates 1, 2, and 3. It is readily seen in these photomicrographs that the hypodermal layer is composed of only a few rows of cells in needles from the Siskiyou locality, which has a mild climate, and of many rows in needles from the Ashley locality, which has a severe climate. Similarly the former are seen to have little depression of the stomata, whereas the latter have deeply depressed stomata. It is evident that the degree to which the openings of stomatal chambers are sunk below the general level of the leaf surface corresponds to the number of rows of cells in the hypoderm. Table 6 presents data on these two characteristics.

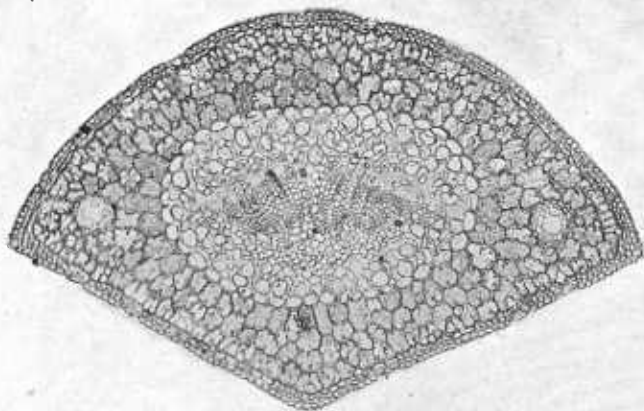
From the table and the plates it appears that, in general, hypoderm-cell and stomatal-depression characteristics have been inherited by the progenies in the new habitat and retained by them. A slight variation in degree of inheritance seems to be indicated in progenies derived from localities in the south plateau region and east of the Continental Divide, which have climates more rigorous than that of the experimental site on the Kaniksu Forest. Needles of these progenies tend to have somewhat fewer rows of hypoderm cells and slightly less stomatal depression than do needles in the parent localities.

When the localities are grouped by similarity of the hypodermal and stomatal characteristics described, as in table 6, they fall into three distinct main groups: (1) The North Pacific locality by itself, (2) the north plateau localities, and (3) all the localities of the central and south plateaus and the region east of the Continental Divide. Again the Helena locality is intermediate, resembling the north plateau localities more than the others.

Table 7 presents data on two other features of needle structure—relative thickness of walls in inner rows of hypoderm cells and percentage of thick-walled cells in inner hypoderm rows. According to the available evidence, each of these characteristics may be regarded as inherited.

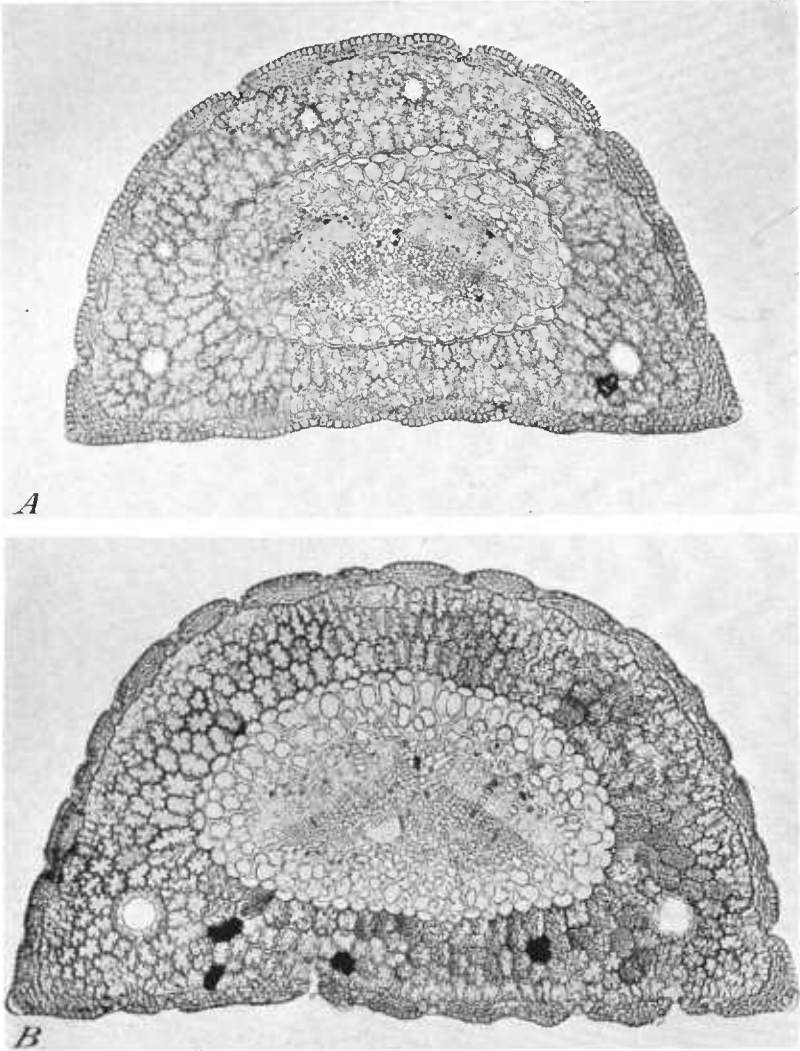


A



B

Cross sections of needles of Siskiyou trees, showing thin layer of hypoderm cells and little stomatal depression: *A*, Needle from parent locality; *B*, needle from progeny plot. Note the similarity between *A* and *B*, indicating inheritance of these characteristics in the new environment. These specimens are typical of the foliage of Siskiyou trees and closely resemble specimens typical of the foliage of north plateau trees. $\times 110$.



Cross sections of needles of Ashley trees, showing thick layer of hypoderm cells and deeply depressed stomata: *A*, Needle from parent locality; *B*, needle from progeny plot. Note the similarity between *A* and *B*, indicating inheritance of these characteristics in the new environment. These specimens are typical of the foliage of trees of the region east of the Continental Divide and the central and south plateau regions. $\times 110$.

TABLE 6.—*Number of inner rows of hypoderm cells containing thickened cell walls and depression of stomata in needles on progeny plots and in parent localities*

Climatic region and locality of seed origin	Inner rows of hypoderm cells containing thickened cell walls		Depression of stomata		Group characteristics	
	Progeny plot	Parent locality	Progeny plot	Parent locality	Rows containing thickened cell walls	Depression of stomata
North Pacific: Siskiyou.....	Number 1, 2	Number 1, 2	None.....	None.....	Few.....	None.
North plateau:						
Boise.....	1, 2, 3	1, 2, 3	Moderate.....	None, moderate.	Few to moderate.	Slight to moderate.
Payette.....	1, 2, 3	1, 2, 3	do.....	do.....		
Whitman.....	1, 2	1, 2, 3	None, moderate.	do.....		
Umatilla.....	1, 2	1, 2, 3	Moderate.....	do.....		
Colville.....	1, 2	1, 2, 3	None, moderate.	do.....		
Kaniksu.....	1, 2	1, 2	do.....	do.....		
Lolo.....	1, 2, 3	1, 2	do.....	Moderate.....		
Bitterroot:						
4,000 feet.....	1, 2	1, 2, 3	do.....	do.....		
5,000 feet.....	1, 2, 3	1, 2	Moderate.....	None, moderate.		
7,200 feet.....	2, 3	1, 2	do.....	do.....	Many.....	Deep.
East of Continental Divide:						
Helena.....	1, 2, 3	1, 2, 3	do.....	Moderate, deep.		
Custer.....	2, 3, 4	3, 4, 5	Deep.....	do.....		
Harney.....	2, 3, 4	2, 3, 4	do.....	Deep.....		
Roosevelt.....	2, 3, 4	3, 4, 5	do.....	do.....		
San Isabel.....	1, 2, 3, 4	2, 3, 4, 5	do.....	do.....		
South plateau:						
Coconino.....	2, 3	3, 4, 5	do.....	do.....		
Santa Fe.....	2, 3, 4	3, 4	do.....	Moderate.....		
Central plateau: Ashley.....	2, 3, 4, 5	2, 3, 4, 5	do.....	Deep.....		

TABLE 7.—*Relative thickness of walls in inner rows of hypoderm cells and proportion of thick-walled cells in hypoderm of needles on progeny plots and in parent localities*

Climatic region and locality of seed origin	Relative thickness of cell walls ¹		Proportion ² of hypoderm cells having thick walls		Group characteristics	
	Progeny plot	Parent locality	Progeny plot	Parent locality	Cell-wall thickness	Cells having thick walls
North Pacific: Siskiyou.....	I, II	I	F, M	F, M	Mostly thin...	Few.
North plateau:						
Boise.....	II	I, II	M, A	M, A	Mostly thin to thick.	Moderate to many.
Payette.....	I, II, III	I, II	M, A	M		
Whitman.....	I, II, III	I, II	M	M, A		
Umatilla.....	I, II, III	I, II	M	A		
Colville.....	I, II	I, II	M	M		
Kaniksu.....	I, II	I, II	M	M, A		
Lolo.....	I, II	I, II	M	A		
Bitterroot:						
4,000 feet.....	I, II	II	M	M, A		
5,000 feet.....	II	II	M	M, A		
7,200 feet.....	II	II	M, A	M, A	Mostly thick.	Practically all.
East of Continental Divide:						
Helena.....	II, III	II	M, A	M, A		
Custer.....	II, III	II, III	A	M, A		
Harney.....	II, III	II, III	A	A		
Roosevelt.....	II, III	II, III	A	A		
San Isabel.....	II, III	II, III	A	A		
South plateau:						
Coconino.....	II, III	II, III	A	A		
Santa Fe.....	II, III	II, III	A	M, A		
Central plateau: Ashley.....	II, III	II, III	A	A		

¹ I=thin, or only slightly thicker than cell walls of epidermis; II=thick, or conspicuously thicker than cell walls of epidermis; III=very thick, or so thick as almost to eliminate lumen.

² As determined along perimeters of cross sections of needles. Includes all cells having thick or very thick walls. F=0-50 percent; M=51-99 percent; A=all, or 100 percent.

It will be noted that the localities fall into the same three groups on the basis of these characteristics as of those in table 6, and that the Helena locality is intermediate here also, with closer resemblance to the north plateau localities than to the others east of the Continental Divide.

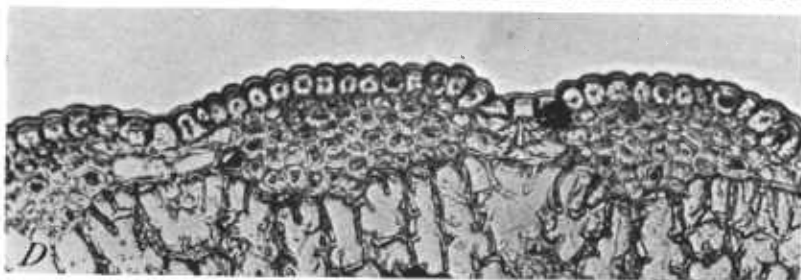
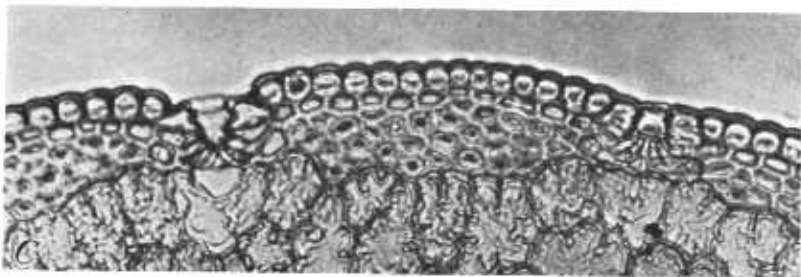
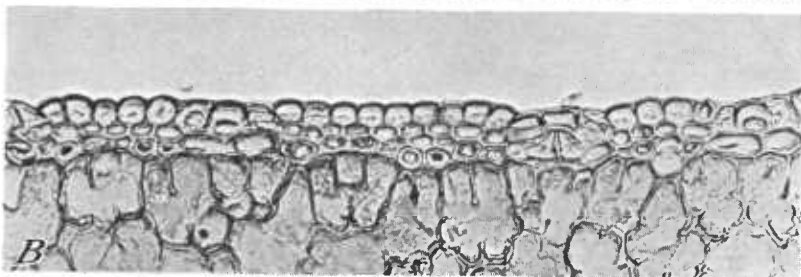
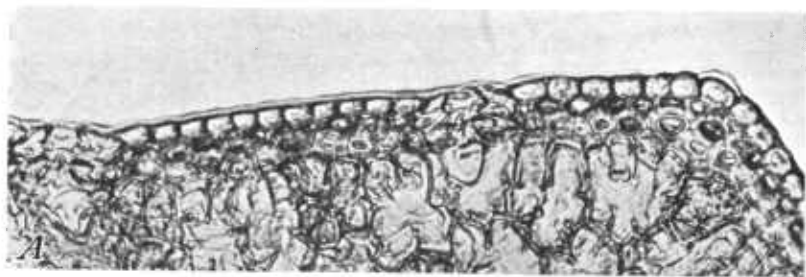
GENERAL APPEARANCE OF FOLIAGE

Even casual observers of the progeny plots have noticed many differences among the various progenies in general appearance of foliage. Corresponding differences are observed among the trees of the parent localities. The typical foliage appearance of the North Pacific and north plateau progenies is exemplified by the Umatilla progeny, illustrated in plate 4, *A*, and that of the progenies from east of the Continental Divide and from the central plateau by the Roosevelt progeny, illustrated in plate 4, *B*. Trees of the former group have relatively long, slender, flexible needles, typically occurring in fascicles of three, arranged on the branches in rather open plumes. Those of the latter have stiff, short, coarse needles, typically occurring in fascicles of two,⁶ arranged more compactly on the branches and in many cases curved toward the stem. The foliage appearance of the south plateau progenies, illustrated in plate 4, *C*, is intermediate.

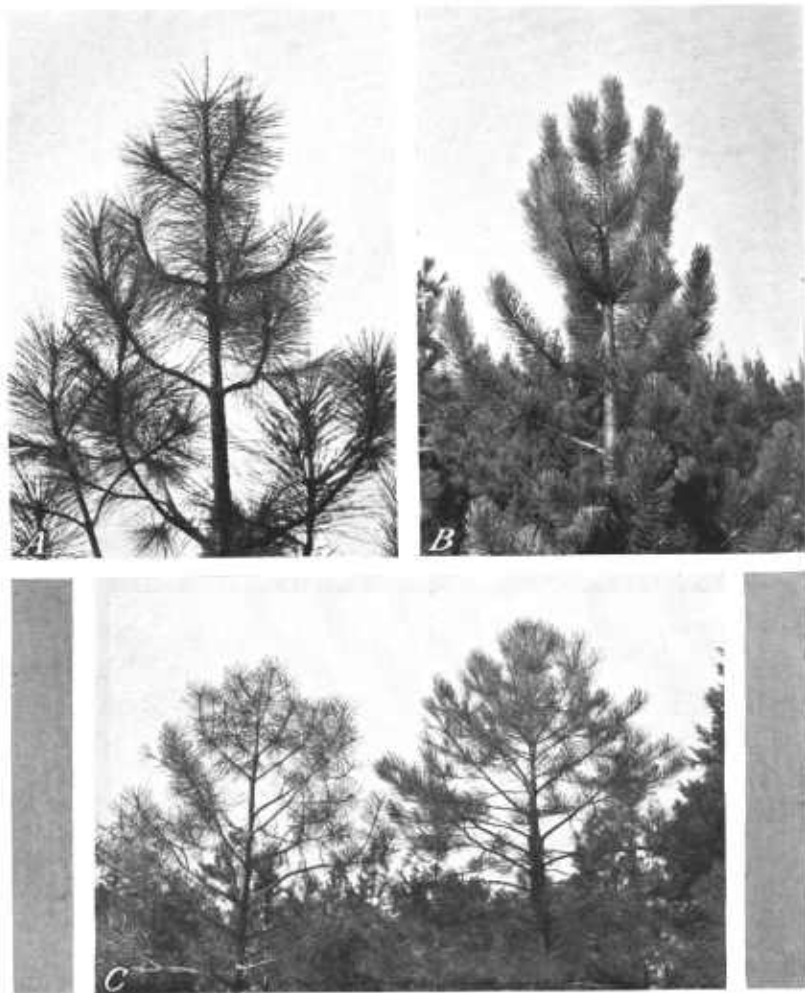
Thickness and stiffness of the needles are roughly proportional to quantity of stiffening tissue in the hypoderm, data on which are shown in tables 6 and 7. The foliage of the Coconino and Santa Fe stocks, in spite of heavy strengthening of the hypoderm, has an open appearance as compared with that of progenies or native trees of either the central plateau or the region east of the Continental Divide. This is accounted for by moderate length and relative slenderness of needles.

It is difficult to make distinctions as to color of foliage, because color is elusive and apparently varies to some degree with season, site, and health of the tree, and because the current year's foliage is often brighter in hue than the older foliage. In general, as seen from a distance, the foliage of the North Pacific and north plateau progenies is medium green to slightly yellow green and that of the progenies from east of the Continental Divide and from the central and south plateaus is gray green. On the basis of Ridgway's color charts (26), the progenies' foliage on the internode of the current season was classified in August 1936 as follows: Spinach green—Siskiyou, Kaniksu, Lolo, Bitterroot 4,000, Bitterroot 5,000, Bitterroot 7,200, Boise, Payette, Whitman, Umatilla, Colville, Coconino, Santa Fe, and Helena; light elm green—Roosevelt, Harney, Custer, and San Isabel; biscay green—Ashley. On the same basis their foliage on the internodes of earlier seasons was classified at that time as follows: Varney's green—Siskiyou, Kaniksu, Lolo, Bitterroot 4,000, Bitterroot 5,000, Bitterroot 7,200, Boise, Payette, Whitman, Umatilla, and Colville; deep dull yellow green—Coconino, Santa Fe, and Helena;

⁶ The Ashley progeny in this group, with only 39.8 percent of its fascicles containing two needles, may still be said to be strongly two-needled in character. In contrast, in all the progenies classified as three-needled, the fascicles containing two needles amount to less than 8 percent.



Sections of needles from Siskiyou (A) native tree and (B) progeny tree, characteristically containing few rows of hypoderm cells, and sections of needles from Ashley (C) native tree and (D) progeny tree, characteristically containing many rows of hypoderm cells. $\times 650$.



342,213-348,463-313,688

Foliage characteristics of progenies: *A*, Open, plumelike arrangement of long, slender needles of Umatilla progeny, typical of the north plateau and north Pacific regions; *B*, compact, brushlike arrangement of short, thick needles of Roosevelt progeny, typical of the region east of the Continental Divide and the central plateau region; *C*, intermediate foliage characteristic of Santa Fe progeny, typical of the south plateau region.

pois green—Roosevelt, Harney, Custer, and San Isabel; light elm green—Ashley. A general correspondence in color was observed between trees of parent localities and progenies.

A purple bloom was found on tree branches collected in the Coconino and Santa Fe localities. On the progeny plots, in northern Idaho, a similar bloom appeared on twigs of Santa Fe, San Isabel, and Ashley trees but was not observed on Coconino trees.

GROUPING ACCORDING TO FOLIAGE CHARACTERISTICS

It is evident from the data presented in tables 3–7 that the localities of seed origin having similar foliage characteristics fall into a few groups, and that these groups are closely related to the climatic regions shown in figure 1. Table 8 summarizes these data.

It will be noted from table 8 that trees with preponderantly three-needle fascicles and long or moderately long, slender, flexible needles are found in the North Pacific, north plateau, and south plateau regions. Readily recognized differences in hypoderm structure, reflecting climatic differences, cause this group to subdivide into its three regional parts; hypoderm tissue is little or not at all thickened in the North Pacific trees, moderately thickened in the north plateau trees, and heavily thickened in the south plateau trees.

Trees having a preponderance of two-needle fascicles and distinctly short, thick, stiff needles with heavily thickened hypoderm tissue are typical of the region east of the Continental Divide.

In the Ashley and Helena localities foliage is intermediate in character. Needles of Ashley trees, in the central plateau region, are short, thick, and stiff and have heavy hypoderm structure, like those of trees east of the Divide. The central plateau trees resemble the south plateau trees in having more three-needle than two-needle fascicles. All factors considered, however, they are more closely related to those east of the Divide. The foliage of Helena trees is intermediate in needle length and hypoderm structure between typical foliage east of the Divide and that on the north plateau, but the similarity to the latter is much closer. This together with strong three-needle fascicle occurrence aligns the Helena trees with those of the north plateau. The Helena locality is only 15 to 20 miles east of the Divide, near enough to be affected by west side conditions.

Although no progenies from the South Pacific region are represented in this experiment, foliage data are available from specimen branches obtained from four trees at Quincy, in north central California. Collection and study of the branch material followed the procedure described for studying the foliage characteristics of trees in parent localities. The foliage of the Quincy trees had 99 percent of three-needle fascicles, and long, slender, flexible needles. Average length of needles was 7.3 inches, and principal range was 6.6 to 8.1 inches, longer than any measured in the experiment. Inner rows of hypoderm cells containing thickened tissue were few to moderate in number, the cell walls were only slightly to moderately thick, and stomata were but slightly to moderately depressed. All these characteristics are typical of the trees of the North Pacific and north plateau regions.

TABLE 8.—Summary of foliage characteristics by regions, based on progeny trees and trees in parent localities

Region or locality of seed origin	Typical appearance of foliage	Fascicles		Needle length			Hypodermal thickening
		General type	Having 3 needles	General type	Principal range	Average	
North Pacific.....	Needles long, slender, flexible. Foliage plumelike. Medium green to yellow green.	Typically 3-needed.	Percent 90-100	Long	Inches 4.8-7.6	6.2	Very little.
North plateau.....	do.	do.	90-100	do.	4.6-6.9	5.8	Moderate.
Helena.....	Needles moderately long and slender, slightly stiff. Gray green.	do.	70-90	Medium to long.	3.9-7.6	5.8	Moderate to heavy.
South plateau.....	do.	do.	90-100	do.	4.0-6.9	5.4	Heavy.
East of Divide.....	Needles short, thick, stiff. Foliage bristly. Gray green.	Typically 2-needed. Intermediate	10-50	Short.	2.9-5.7	4.3	Do.
Central plateau.....	do.		60-75	do.	3.2-5.2	4.2	Do.

GROWTH CHARACTERISTICS

HEIGHT AND DIAMETER OF PROGENY

The period from the first planting on a given progeny plot to the most recent measurement of the trees, in 1935, varied from 19 to 24 years. In order to compare all the progenies at a uniform age, heights and diameters were computed as of the end of the twentieth season after outplanting. As the nursery stock was in some cases 2 years and in others 3 years old at the time of outplanting, the total ages from seed represented by the height and diameter values thus obtained are 22 and 23 years.

In drawing conclusions from the growth figures, allowance should be made for the influences of density and spacing. All the plots are reasonably comparable in these respects except the Siskiyou, Bitterroot 7,200 feet, and Santa Fe, on which relatively few trees remain and these are widely spaced. As the surviving trees are the best of the individuals planted, at least on the first two plots, their growth is probably somewhat too advanced to be representative.

Table 9 shows for each plot the average height, the standard deviation of heights, and the extremes of height. Despite the uniformity of the site on which the trees are growing, there are wide differences in height growth. Average heights range from 15.7 feet for the Lolo to 7.2 feet for the Ashley progeny. In general the progenies derived from localities near the site of the experiment have made the best height growth. Those derived from the highest altitudes have in general made the least growth. These results are in agreement with those of European investigations (5, 8, 9, 12, 35).

TABLE 9.—*Height of progeny trees after 20 years' growth on plots*¹

Region, locality, and altitude (feet) of seed origin	Average	Standard deviation	Standard error	Maximum	Minimum	Basis, trees
	<i>Feet</i>	<i>Feet</i>	<i>Feet</i>	<i>Feet</i>	<i>Feet</i>	<i>Number</i>
North Pacific: Siskiyou (2,000).....	11.9	±4.5	±0.95	19.5	4.0	22
North plateau:						
Boise (5,500).....	10.4	±4.2	±.50	27.5	3.0	71
Payette (5,000).....	10.5	±2.7	±.40	19.0	3.5	45
Whitman (5,000).....	9.4	±3.7	±.65	20.0	4.0	33
Umatilla (3,500).....	11.7	±3.4	±.56	19.0	3.5	37
Colville (2,700).....	12.4	±4.1	±.44	21.0	4.5	86
Kaniksú (2,600).....	12.6	±3.9	±.50	21.0	1.5	61
Lolo (3,000).....	15.7	±4.9	±.54	26.0	6.5	81
Bitterroot:						
4,000.....	14.5	±4.1	±.51	22.0	6.0	65
5,000.....	13.1	±3.7	±.40	23.0	2.5	86
7,200.....	11.4	±4.6	±.76	21.0	3.5	36
East of Continental Divide:						
Helena (4,500).....	12.8	±3.4	±.36	21.0	6.0	87
Custer (3,200).....	9.8	±3.0	±.35	15.5	4.0	70
Harney (5,000).....	11.1	±4.9	±.55	17.0	4.0	79
Roosevelt (8,000).....	8.6	±2.6	±.50	15.5	5.0	27
San Isabel (8,000).....	9.0	±2.8	±.47	15.0	4.5	36
South plateau:						
Coconino (7,100).....	9.0	±2.6	±.33	15.5	4.5	63
Santa Fe (8,000).....	7.5	±2.4	±.54	11.0	3.0	20
Central plateau: Ashley (7,500).....	7.2	±2.6	±.37	12.0	1.5	49

¹ As the progeny trees were 2 and 3 years old when planted on the plots, the total ages represented by these measurements are 22 and 23 years.

Average diameters at breast height (4.5 feet above ground) 20 years after outplanting were read from height-diameter curves made for all plots (table 10). They ranged from 3.0 inches for the Lolo progeny to 1.2 inches for the Santa Fe and Ashley progenies. Table 11 presents average heights and diameters of dominant trees.

TABLE 10.—*Diameter of progeny trees after 20 years' growth on plots*¹

Region, locality, and altitude (feet) of seed origin	Average	Standard deviation	Standard error	Basis, trees
	<i>Inches</i>	<i>Inches</i>	<i>Inches</i>	<i>Number</i>
North Pacific: Siskiyou (2,000)-----	2.8	±1.5	±0.32	21
North plateau:				
Boise (5,500)-----	2.1	±1.4	±.17	68
Payette (5,000)-----	2.0	±1.3	±.19	44
Whitman (5,000)-----	1.8	±1.3	±.23	30
Umatilla (3,500)-----	2.2	±1.5	±.25	36
Colville (2,700)-----	2.4	±1.4	±.16	85
Kaniku (2,600)-----	2.6	±1.2	±.15	58
Lolo (3,000)-----	3.0	±1.3	±.15	81
Bitterroot:				
4,000-----	2.9	±1.1	±.22	65
5,000-----	2.5	±1.2	±.13	85
7,200-----	2.3	±1.1	±.19	35
East of Continental Divide:				
Helena (4,500)-----	2.0	±1.2	±.13	87
Custer (3,200)-----	1.4	±1.1	±.13	70
Harney (5,000)-----	2.0	±.7	±.08	78
Roosevelt (8,000)-----	1.5	±1.3	±.24	27
San Isabel (8,000)-----	1.7	±1.2	±.21	36
South plateau:				
Coconino (7,100)-----	1.8	±1.2	±.15	63
Santa Fe (8,000)-----	1.2	±1.0	±.02	16
Central plateau: Ashley (7,500)-----	1.2	±.9	±.01	43

¹ See footnote 1, table 9.TABLE 11.—*Average height and diameter of dominants among progeny trees after 20 years' growth on plots*¹

Region, locality, and altitude (feet) of seed origin	Height	Diameter	Basis, trees	Region, locality, and altitude (feet) of seed origin	Height	Diameter	Basis, trees
	<i>Feet</i>	<i>Inches</i>	<i>Number</i>		<i>Feet</i>	<i>Inches</i>	<i>Number</i>
North Pacific: Siskiyou (2,000)-----	17.3	4.5	7	East of Continental Divide:			
North plateau:				Helena (4,500)-----	16.6	3.1	28
Boise (5,500)-----	17.2	4.2	13	Custer (3,200)-----	13.6	2.4	9
Payette (5,000)-----	13.8	3.1	11	Harney (5,000)-----	13.8	2.9	23
Whitman (5,000)-----	15.0	3.8	6	Roosevelt (8,000)-----	12.3	2.8	6
Umatilla (3,500)-----	15.3	3.4	11	San Isabel (8,000)-----	13.2	3.1	7
Colville (2,700)-----	17.4	4.2	26	South plateau:			
Kaniku (2,600)-----	16.5	3.9	20	Coconino (7,100)-----	12.8	3.2	13
Lolo (3,000)-----	21.3	4.6	24	Santa Fe (8,000)-----	9.7	2.2	6
Bitterroot:				Central plateau: Ashley (7,500)-----	10.9	2.5	8
4,000-----	18.3	4.0	23				
5,000-----	17.3	3.7	22				
7,200-----	17.2	3.9	10				

¹ See footnote 1, table 9.TABLE 12.—*Regional averages of height and diameter of progeny trees after 20 years' growth on plots*¹

Region or locality of seed origin	Average height ²	Range of plot heights	Average diameter ²	Basis, plots	Region or locality of seed origin	Average height ²	Range of plot heights	Average diameter ²	Basis, plots
	<i>Feet</i>	<i>Feet</i>	<i>Inches</i>	<i>Number</i>		<i>Feet</i>	<i>Feet</i>	<i>Inches</i>	<i>Number</i>
North Pacific-----	11.9		2.8	1	East of Continental Divide-----	10.0	8.6-11.1	1.7	4
North plateau-----	12.5	9.4-15.7	2.4	10	South plateau-----	8.6	7.5-9.0	1.7	2
Helena-----	12.8		2.0	1	Central plateau-----	7.2		1.2	1

¹ See footnote 1, table 9.² Regional values shown are weighted averages of locality averages.

In table 12 a comparison is made among the regions as to average heights and diameters of progeny. Statistical analysis by the method of variance shows no significant differences in average height

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Stand views of progeny plots in 1935: *A*, Straight, tall, well-formed stems of Lolo progeny; *B*, slightly crooked and rapid-tapering stems, open branches, and rounded slow-growing tops of Coconino progeny.



General view of Bitterroot 5,000 plot in 1932, showing tree form and pointed crowns typical of north plateau progenies.

between North Pacific progeny (1 plot), north plateau progenies (10 plots), and Helena progeny (1 plot). On the other hand, the difference in average height between progenies derived from localities east of the Continental Divide (4 plots) and north plateau progenies is statistically significant, and so are the differences between south and north plateau progenies and central and north plateau progenies. Thus it is shown that the progenies derived from the south and central plateaus and the region east of the Continental Divide are truly of slow growth in northern Idaho.

RELATION OF HEIGHT TO DIAMETER

Another growth characteristic of interest to the forester is the height-diameter relation, which reflects capacity to make volume and quality growth. In the absence of data for the determination of form factors, height as related to diameter at breast height was taken from the curve made for each plot. The data are presented in figure 4.

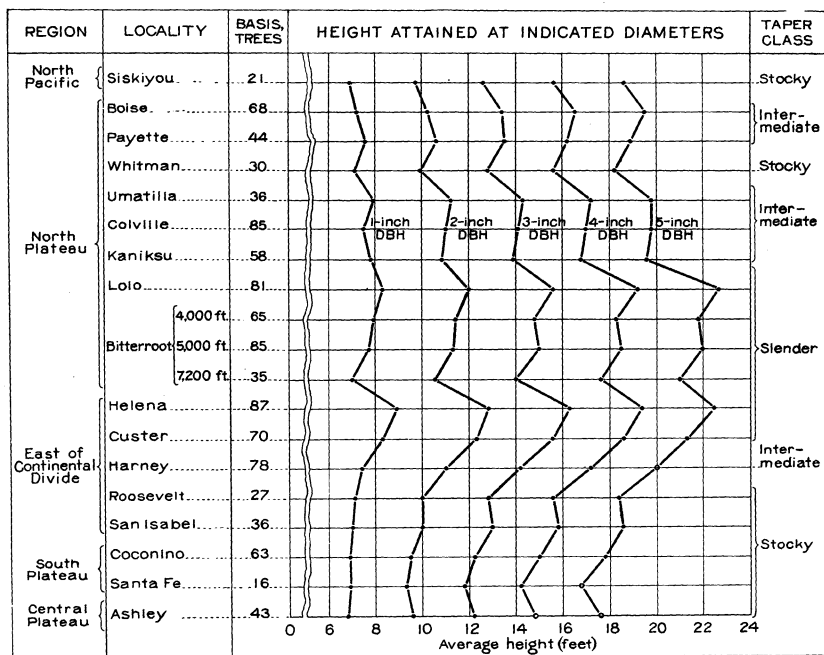


FIGURE 4.—Relation of average height of progenies to diameter in the various plots. (Dots indicate actual and circles interpolated data.)

Great differences in form are evident. For example, average height of trees 5 inches in diameter is 22.7 feet on the Lolo plot but only 16.8 feet on the Santa Fe plot. The range of differences was divided into three equal parts representing the three taper classes slender, stocky, and intermediate, of which slender is the most desirable and stocky the least desirable. Progenies in the slender class are the Lolo, Helena, Custer, and Bitterroot; those in the stocky class are the Santa Fe, Ashley, Coconino, Roosevelt, San Isabel, Whitman, and Siskiyou. Plate 5 presents examples of progenies having (A) well-formed stems and (B) poorly formed stems. Plate 6 shows the general form and

pointed crowns of a typical north plateau progeny. (Compare with pls. 4, *C*, and 5, *B*, illustrating the characteristic rounded crowns of typical south plateau progenies.) Attention is again called to the wide spacing of the surviving trees of the Siskiyou and Santa Fe progenies; it is not known what differences their stem forms would show if they had developed in closed stands.

It is believed that the data for ages 22 to 25 years represent the height-diameter ratios of most of the trees from youth to maturity. Because of comparatively early falling off of height growth in the Custer and Harney parent localities, however, it is reasonable to assume that the stem form of the two progenies will deteriorate later in life. On the other hand, the Whitman and Siskiyou progenies may be expected to continue height growth longer and improve in stem form, like the trees in their parent localities.

RELATIVE HEIGHT GROWTH BY YEARS

In studying introduced species and races, foresters both in Europe and in the United States have been inclined to judge the relative growth possibilities of different progenies from their behavior during

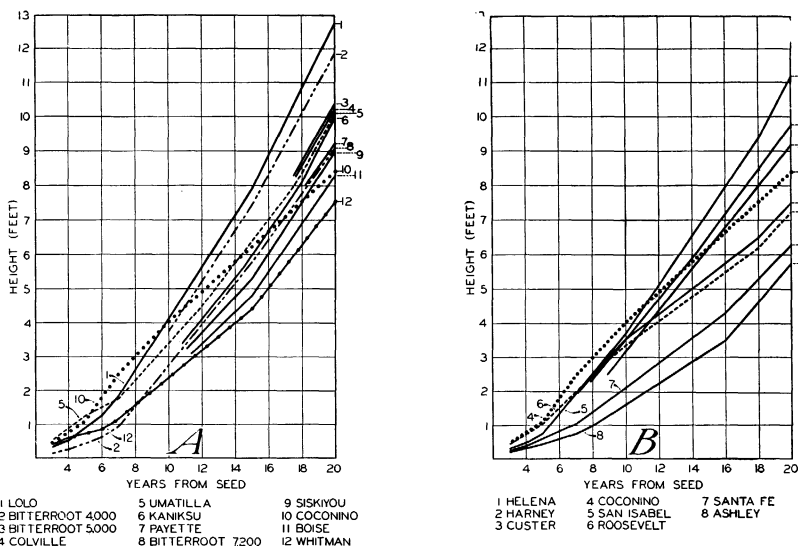


FIGURE 5.—Relative height growth, by year, of progenies derived (A) from North Pacific and north plateau sources, and Coconino; and (B) from south and central plateau and east of Continental Divide. Sources are indicated by number.

the first few years. This has not always been justified by the character of growth made in later years. Some introduced races that have made strikingly rapid height growth in the first few years have later fallen behind local races. The height measurements taken annually from 1912 to 1919 and those taken in 1927 and 1935 have made it possible to plot curves that show effectively the trends of early height growth in this experiment.

The height curves of the north plateau and North Pacific progenies and the Coconino progeny, given in figure 5, A, show that the Coconino progeny grew faster than any of the others during the first 10

years. Gradually, however, its growth rate has become less rapid, and local races have been overtaking it. The Lolo progeny, which in 1935 was growing more rapidly than any other, passed it at 10 years, the Bitterroot 4,000 at 11 years, the Umatilla at 14 years, and most of the others by 18 years.

Figure 5, *B*, shows that the Coconino progeny was foremost in height growth among the progenies derived from the central and south plateaus and from east of the Continental Divide, until the Helena, Harney, and Custer progenies overtook it between 11 and 15 years. The Roosevelt, San Isabel, and Umatilla progenies also excelled in height growth at the start but were soon overtaken by local progenies.

This comparison is evidence that initial growth rate of introduced races should not be accepted as presaging the later development of the trees. The trends shown here may, indeed, be taken as a warning not to apply too far into the future the present conclusions from results at 22 to 26 years of age.

GROWTH OF PROGENIES COMPARED WITH GROWTH IN PARENT LOCALITIES

If an experiment such as that described here shows, for example, that a given introduced race is much slower in growth than a local race, and therefore unsuitable for planting as a timber crop, this indication ordinarily meets the needs of the practicing forester. The findings are much more valuable, however, if they indicate further whether the growth rate of the introduced race is hereditary or is due to a difference in environment. As one of the purposes of this experiment is to determine what characteristics are heritable, an effort has been made to ascertain the growth rates of ponderosa pine in the parent localities.

Suitable growth data have been made available for the general localities of seed origin through a recent interregional yield study⁷ of even-aged ponderosa pine stands in the northern part of the range of the species, from the Black Hills to California. The data used in this yield study included average heights of dominant and codominant trees by decades for each of 13 site classes. From these data and from measurements yielding average site indices made in the general localities of seed origin, it was possible to plot the curves for this portion of the range shown in figure 6, *A*. As the basic data were intended solely for use in constructing yield tables, they were deficient in measurements of stands less than 25 years old. Therefore the lower portions of the curves had to be constructed by extension, and the heights indicated are close approximations only. These curves are sufficiently accurate, however, to serve in comparing rates of growth in the different localities. The curve shown in figure 6, *A*, for Arizona and New Mexico (south plateau) was plotted from growth measurements made by H. M. Curran, in his report already cited. Data on rates of growth are not available for the specific localities of seed origin in Utah, Colorado, or western Oregon.

To construct figure 6, *B*, average heights of dominant and codominant progeny trees at 20 years were plotted and a straight line was drawn from each plotted height to the origin point.

⁷ This study was supervised by W. H. Meyer, then of the Pacific Northwest Forest and Range Experiment Station, and the site-index data here used were supplied by him. The contribution to this study from the Northern Rocky Mountain Region consisted of data on 101 yield plots in northern Idaho, 99 in western Montana, and 35 in eastern Montana.

In studying figure 6 it will be seen that the curves representing the western Montana, northern Idaho, and southern Idaho stocks occupy the upper part of the growth range both of native trees and of progeny trees, and that the curves for eastern Montana, Black Hills, and south plateau stocks occupy the lower part of each range. The curve for the Arizona and New Mexico trees is lower than all the others in *A*, and conspicuously so in *B*.

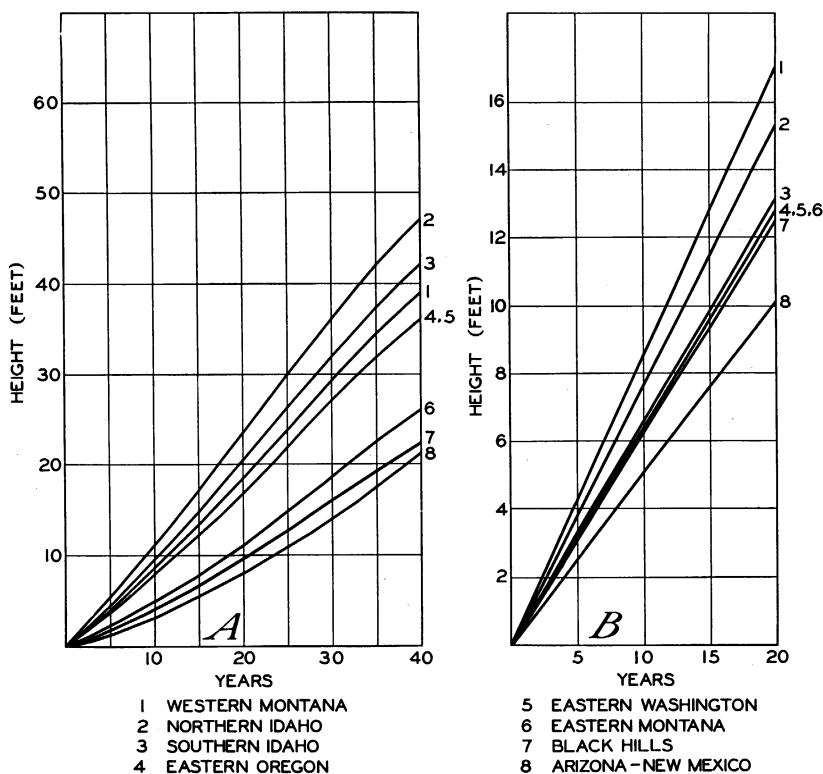


FIGURE 6.—Average heights of dominant and codominant trees (*A*) of some of the parent localities and (*B*) of some of the progeny plots. Seed sources are indicated by number.

It appears that progenies from localities of more severe climate than northern Idaho have inherited the slow growth rates typical of such localities. This agrees with findings of numerous European investigations (5, 6, 8, 12, 18, 35). As shown by the present study, the inheritance is strongly maintained through more than 20 years of the first generation. More extended experiments in Europe described by Dengler (9) and Münch (21) indicate that inherited growth characteristics are maintained also in trees of the second generation of introduced races.

In the single case (Siskiyou) of a progeny originating in a climate considerably milder than that of the experimental site in northern Idaho, the rapid growth rate of trees in the region of origin was not exhibited by the progeny. The site indices for the northern Sierra

territory, embracing the Siskiyou and Shasta seed-source localities (not included in fig. 6), are much higher than those for any other part of the range of ponderosa pine included in this study. The Siskiyou progeny trees surviving the severe winter freeze in 1924 that killed all the Shasta progeny have grown fast, but not so fast as trees in the parent locality. This indicates the inhibiting influence of climatic conditions more severe than those of the parent habitat. Büsgen and Münch (6), Dengler (9), and others have pointed out similar results of introducing races from a mild climate to a cold one. There is here, of course, no indication that progeny of the same Siskiyou parent trees would fail to inherit rapid growth rate if planted in localities of mild climate. Rate of growth is a quantitative characteristic that is modified by environment as well as by inheritance.

PHENOLOGICAL CHARACTERISTICS

Among the factors that have an important bearing on the adaptability of progeny to a given climate, in addition to needle structure, are the parent trees' characteristics as to time of beginning and ending seasonal growth. In this connection Büsgen and Münch (6) state:

Races of trees from regions with a short growing season and bad forest growth, when transplanted to mild situations, retain the short duration of their vegetation, fail to utilize the longer growing season, and so remain behind the indigenous local races. In general they come into leaf earlier, it is true, because less heat suffices for their vegetation, but they cease their growth early in the summer. When the transfer is in the opposite direction the trees seek to retain their inherited long vegetative period, grow on into the autumn and perish with frost.

That vigor of growth and susceptibility to disease as well as to frost are in large measure determined by inherited phenological habits has been shown by many investigators (5, 8, 9, 12, 18, 19, 20, 34).

Phenological observations have not been made on the progeny plots, but have been conducted for 8 years on native conifers near the experimental site. They show that the date when the buds on indigenous ponderosa pine begin to burst ranges from April 12 to May 25, averaging April 29. In the Coconino parent locality, Pearson (25) observed during a period of 3 years that buds of ponderosa pine begin to burst from May 15 to May 25. Thus the growing season of the Coconino locality begins about 3 weeks later than that of the Kaniksu locality. The fact that the Coconino progeny has a short period of vegetative activity presumably has been one cause of the comparatively small growth it has attained at 20 years (fig. 5, B). On the other hand presumably the long period of growth activity characteristic of trees in the North Pacific region, transmitted to the Siskiyou progeny, has been one of the causes of the frost damage suffered by the latter in northern Idaho.

GEOGRAPHIC RACES INDICATED

The data on foliage and growth characteristics obtained in this study, together with information on climate in different parts of the range of ponderosa pine, clearly point to the existence of several forms or races. The grouping of localities of seed origin by similar foliage characteristics and the discussion in that connection have already indicated general racial trends. It remains to present

evidence contributed by an examination of climate and growth characteristics. Fine distinctions are not attempted. It is realized that in addition to the characteristics studied, racial distinctions depend also upon differences in cones,⁸ bark, and wood, disease resistance, and other factors not dealt with in this study. The data most indicative of racial differences are shown in tables 8 and 12. In this connection, attention is directed also to figures 1 and 2 and to tables 1 and 2.

NORTH PACIFIC REGION

Trees of the North Pacific region differ from those of the remainder of the ponderosa pine range chiefly in that they are adapted to a mild, equable climate and are poorly equipped to withstand low temperatures. Their leaf structure is distinct from that of the trees of any other region studied, since very few of the hypoderm cells have thick walls. In this region extremely low temperatures are unknown, and the frostless season is longer and total precipitation much greater than in any of the other ponderosa pine regions studied. The fact that all the progeny trees derived from one of the two seed-source localities in this region and most of those from the other died as a result of the precipitous drop in temperature on December 15, 1924, from 45° F. to -12° F. in 20 hours, may be traced to the absence of protective hypodermal thickening. Both rainfall and precipitation effectiveness are high in the North Pacific region, and growth is consequently better there than in any of the other regions. The evidence seems to indicate that the ponderosa pine of the North Pacific region is a race by itself.

NORTH PLATEAU REGION

The foliage of the north plateau trees resembles that of the North Pacific trees in length, slenderness, and flexibility of needles and in occurrence of three-needle fascicles, but it has a distinct moderate hypodermal thickening, which presumably has a part in enabling the trees to resist severe low temperatures better than those of the North Pacific region. The progenies derived from this region suffered little loss from the freeze of December 15, 1924. Growing-season precipitation and temperature are favorable and growth in the parent localities is better than in any of the other regions studied except the North Pacific. The growth of many of the progenies greatly excelled that of progenies from other regions. On the basis of structural adaptation to low temperatures, the north plateau trees constitute a race distinct from the North Pacific trees.

REGION EAST OF CONTINENTAL DIVIDE

As already brought out, the external foliage characteristics of progeny and native trees of the region east of the Continental Divide differ conspicuously from all others in this experiment except those of the Ashley locality in Utah. The outstanding characteristics of the foliage of ponderosa pine in this region are the prevailing occurrence

⁸ Until 1936, cones were borne by the progeny trees only singly and sporadically. Counts in 1936 showed that 11 percent of the Helena trees bore 84 cones; 7 percent of the Roosevelt trees, 24 cones; 3 percent of the Umatilla trees, 9 cones; 2 percent of the Payette, 15 cones; 2 percent of the Kaniksui, 12 cones; and 2 percent of the Lolo, 3 cones.

of two-needle fascicles, the shortness, thickness, and stiffness of the needles and their compact arrangement on the branches, and the large number of rows of cells and heavy thickening of the cell walls in the hypoderm. Rate of growth is mostly slow. The progenies derived from this region have displayed a high degree of hardness (14). Altogether these distinctive characteristics make this a strongly demarcated race.

SOUTH PLATEAU REGION

In moderate length and slenderness of needles and in percentage of three-needle fascicles, the trees of the south plateau show relationship to those of the north plateau and North Pacific regions. The southern form, however, is distinctly different in its conspicuously heavy thickening of hypoderm cells, slightly stiff rather than flexible needles, and much slower rate of growth. The south plateau trees differ also from the trees typical of the region east of the Continental Divide, although internal leaf structure is the same in both forms. Existence of a distinct south plateau race is strongly evident.

CENTRAL PLATEAU REGION

The Ashley locality of seed origin, lying well within the central plateau region, has a lower annual precipitation than any of the other localities of the study, a pronounced deficiency of spring precipitation, and a generally low availability of moisture throughout the growing season. Its annual and summer averages of temperature are among the lowest. Thus precipitation and temperature together form a climate very rigorous for tree growth. This is reflected in the fact that the growth of the Ashley progeny, both in height and in diameter, was less than the average for any regional group of progenies. The needles are short, thick, and stiff and compactly arranged on the branches, as in the region east of the Continental Divide. Number of rows of hypoderm cells and thickness of the cell walls are the greatest found in this study. Foliage occurs mostly in fascicles of three, but many trees contain up to 40 percent of two-needle fascicles.

Thus the trees of this locality have a strong relationship to the trees east of the Continental Divide and have relatively little in common with those of the south plateau. In view of this, the Ashley trees are regarded as of the same race as those east of the Divide.

As indicated by Korstian (16) and by Baker and Korstian (2), the Ashley form of tree is found over much of Utah, Nevada, and the remaining territory included in the central plateau.

HELENA LOCALITY

In the Helena locality, 15 to 20 miles east of the Continental Divide, the foliage is strongly three-needled, with needles of medium length and moderate hypoderm thickening, thus resembling that of the north plateau more closely than that of localities farther east. The height growth of the Helena progeny, moreover, is as great as the average for north plateau trees and outstandingly better than that of other progenies derived from east of the Divide. Altogether, the evidence indicates so close a relationship that the Helena trees may be regarded as belonging to the north plateau race.

RACES SUMMARIZED

Briefly, the races tentatively indicated in this study and their important earmarks are the following:

1. *North Pacific race*.—Typically three-neededled, needles long, very little thickening of hypoderm, rapid growth, relatively low frost resistance.

2. *North plateau race*.—Typically three-neededled, needles long, distinct moderate thickening of hypoderm, good growth, good frost resistance.

3. *South plateau race*.—Typically three-neededled, needles medium to long, very thick hypoderm structure, growth slow, good frost resistance.

4. *Race found east of Continental Divide and on the central plateau*.—Typically two-neededled, needles short, very thick hypoderm structure, growth slow, highly frost-resistant.

Study of foliage from trees at Quincy, Calif., in the South Pacific region (no progeny available) shows fascicles very typically containing three needles. Needles are long and contain moderately thickened hypoderm. The data reveal a very close relationship to the North Pacific and north plateau trees, but are not adequate for ascertaining racial distinctions.

SUITABILITY OF RACES FOR PLANTING IN NORTHERN IDAHO

Decision as to the desirability of a tree race for introduction in a new locality involves consideration of both its adaptability to the local climate and its suitability for timber production. No matter how hardy and disease-resistant a race may be in the new locality, it will be useless for timber-crop production if it grows too slowly and develops a poor, stunted form.

Adaptability to climate unfortunately can be judged only by actual performance; and it has been learned by experience elsewhere that such performance, to be clearly indicative, must extend over at least one-third of the tree's life to maturity. The history of introduced races is replete with instances of break-downs of stands 25 to 40 years after planting. In the classic example described by Wibeck (34), many thousand acres of Scotch pine plantations in Sweden, derived from unsuitable seed sources, died out or developed poor form after having thrived well for 25 or more years. Similar happenings elsewhere in Europe have been reported by numerous writers (3, 7, 9, 11, 13). In South Africa, where the maritime pine (*Pinus pinaster*) of the Mediterranean countries proved to be an excellent species for introduction, Duff (10) shows that more than 285,000 pounds of maritime pine seed were imported between 1898 and 1914 with little or no regard for seed origin. Although many of the plantations have thrived and developed into stands of excellent growth rate and form, others, established with seed from unsuitable sources, at 40 years of age are of slow growth and stunted form or badly infected with disease. In the United States, although forest planting on an extensive scale is not so old, some plantations of introduced species that had an auspicious beginning have already broken down. These include several Scotch pine plantations in Pennsylvania⁹ that made exceedingly rapid, straight, and vigorous growth and gave high promise of being hardy

⁹ AUGHANBAUGH, J. E. SCOTCH PINE—AN ENIGMA. Pa. Dept. Forests and Waters Serv. Letter. 1935.

and adaptable until they were 20 to 25 years old, but then began to disintegrate badly through inability to withstand adverse conditions as to wind, snow, insects, and disease.

Thus it would be premature to make a statement on the ultimate adaptability to northern Idaho and adjacent territory of the progenies introduced in this experiment. Certain present indications of relative adaptability may be pointed out, however, with the warning that some future combination of climatic conditions may upset them.

The chief factors in climatic adaptability and suitability for timber growing are frost hardness, disease resistance, rate of growth, and form. So far the progenies at the northern Idaho experimental site have not been seriously infected with disease and have developed only slight defects in stem form. They have, however, shown marked differences in growth rate and in relative resistance to untimely freezing temperatures.

It is well to keep in mind in this connection that individual parent trees may vary considerably in their ability to produce good or poor progeny in these respects. Although such differences between individual parents may account for some of the variation among trees of a given progeny plot in this experiment, it is believed that the plot averages are fairly safe to use in comparing the relative growth capacity and climatic adaptability of progenies derived from different localities.

The Siskiyou and Shasta stocks, which make rapid growth but are poorly equipped to resist frost, should not be considered for use in northern Idaho; and on the basis of extremely slow growth the Ashley, Roosevelt, San Isabel, Santa Fe, and Coconino stocks, with progeny heights averaging only 7.2 to 9.0 feet at 20 years, should also be excluded, despite the great hardness of most of them. All the progenies other than those derived from the North Pacific region have withstood the severe freezes in northern Idaho during the period covered by this experiment, apparently because of their marked protective thickening of the hypoderm.¹⁰

According to the evidence obtained in this study, a progeny derived from a cold climate and grown in a milder climate exhibits slow growth and immunity to frost; a progeny derived from a mild climate and grown in a colder climate has low frost resistance and fails to exhibit the parental characteristic of rapid growth. Progenies introduced into the North Pacific region from any other part of the range of ponderosa pine would thus be expected to grow more slowly than native trees; and in the central and south plateaus and east of the Continental Divide, progenies introduced from the Pacific coast and the north plateau probably would suffer heavy losses by freezing and would grow more slowly than trees in their parent localities.

Such evidence as is available from similar experiments seems to confirm this reasoning. Near Carson, Wash., in the North Pacific region, in a 14-year-old experiment with ponderosa pine progeny,¹¹ offspring derived from the Bitterroot National Forest, Mont., grew very well but less rapidly than the local races, while progenies of Arizona, New Mexico, and Black Hills origin made the least height growth, as in the northern Idaho experiment. Near Manitou, Colo., in

¹⁰ Evidence of the effect of inherited hypodermal protection, in addition to that afforded by the freeze of December 1924, is the fact that trees in Savenac Nursery, in western Montana, grown from Custer seed, survived an October 1935 freeze with almost no sign of damage, whereas local stocks suffered some damage.

¹¹ Data supplied by the Pacific Northwest Forest and Range Experiment Station.

a 15-year-old experiment with ponderosa pine progenies,¹² the trees of local Roosevelt and San Isabel origin were hardiest and tallest, while those grown from seed derived from the Bitterroot (Mont.) and Tusayan (Ariz.) National Forests were shortest and most subject to losses. Only 5 and 12 percent, respectively, of the latter survived, and their height was only one-third that of the local progenies. Pearson (25) reported that first-year seedlings of ponderosa pine grown in a nursery near Flagstaff, Ariz., from seed collected on the Sierra National Forest, Calif., were completely killed by a November freeze, whereas those grown from seed collected in Arizona, New Mexico, Colorado, and the Black Hills were not injured. In an unpublished report he stated that ponderosa pine progenies grown near Flagstaff from seed collected in various localities in the northern part of the range of the species all died within 5 or 6 years.

Elimination of the Ashley, Roosevelt, San Isabel, Santa Fe, Cocomino, Siskiyou, and Shasta progenies as unsuitable for introduction in northern Idaho leaves 13 progenies, showing excellent to fair growth and having hardiness also in their favor, that must be given consideration as to suitability from a timber-growing standpoint. Ten of these are from localities in the north plateau region and three from localities east of the Continental Divide. Those making rapid height growth are, in order, the Lolo, Bitterroot 4,000, Bitterroot 5,000, Helena, Kaniksu, Colville, Umatilla, and Bitterroot 7,200. The Lolo and Bitterroot 4,000 progenies have a distinct lead over all others in height. The differences among the heights attained by the six other leading progenies are probably not significant, and for the present purpose all six may be regarded as equal in growth capacity. The slower growing of the north plateau progenies thus far are the Payette, Boise, and Whitman.

The Custer and Harney offspring are comparable in rate of growth with the slower growing of the north plateau progenies. As has already been pointed out, in the native localities of these two progenies the height growth of ponderosa pine falls off earlier than in the north plateau region; it is reasonably safe to assume, therefore, that in northern Idaho these progenies will fall far short of the ultimate height growth of trees of local origin. A strong point in their favor is high resistance to sudden drops in temperature below the freezing point (14). It is doubtful, however, whether this advantage can, even in the long run, compensate the faster growth of such local progenies as the Lolo, Bitterroot, Colville, and Kaniksu.

The Helena progeny shows not only a high degree of frost resistance but also a good rate of growth, comparable to those of the Kaniksu and Colville progenies. This indicates the Helena locality as a safe source of seed for planting in northern Idaho when local cone crops are inadequate.

Why the introduced Lolo and Bitterroot 4,000 progenies so definitely surpass the local Kaniksu stock in both growth and hardiness is difficult to explain on the basis of the data now available. Rainfall and temperature records and soil-moisture tests shed but little light on the subject; and as has already been indicated, leaf structure is about the same for all three of these progenies. Perhaps the better part of wisdom would be to keep in mind the example of the rise and fall in height supremacy of the Coconino progeny, shown in figure 5,

¹² Data supplied by the Rocky Mountain Forest and Range Experiment Station.

and not attempt finely drawn explanations of the relative order of these north plateau progenies, on the basis of climatic or any other records.

It would appear that the most suitable general territory in which to collect seed for planting in northern Idaho (and western Montana) extends roughly from the Colville locality, in Washington, to a little beyond the Continental Divide, and from the latitude of the Salmon River approximately to the Canadian boundary.

SUMMARY AND CONCLUSIONS

Trees grown from seed of ponderosa pine collected in 20 localities in the western United States, widely separated geographically or in elevation, were planted on the Kaniksu National Forest, in northern Idaho, in the years 1911-17. Location and climate of the seed sources were known, but no data were recorded as to their soils or the individual characters of parent trees. Measurements of progeny trees were made in each of the years 1912-19, in 1927, and in 1935. At the time of the 1935 measurement the trees were 22 to 26 years old from seed.

A study of external and internal foliage characteristics of the progenies was made as a part of the 1935 examination of the plots. Differences in respect to number of needles to the fascicle, length of needles, general appearance of foliage, and thickening of hypoderm were found among progeny groups derived from five different regions within the range of ponderosa pine in the United States, which were delimited on the basis of precipitation type. These regions were designated North Pacific, north plateau, central plateau, south plateau, and east of the Continental Divide; the sixth region, the South Pacific, was not represented by any of the seed used.

Differences among the progenies in number of needles to the fascicle, length of needles, general appearance of foliage, and rate of growth corresponded to differences among the trees of the parent localities. The conclusion is drawn that these characteristics are strongly heritable in ponderosa pine and will appear in the offspring in any new environment where the trees will grow, at least for more than 20 years of the first generation.

Pronounced differences were exhibited by the different progenies in height and diameter growth. The slowest-growing progenies made only half as much growth as the fastest-growing. The best growth in height and diameter was made by trees derived from localities in the north plateau region resembling the locality of the planting site in climate. The poorest growth was made by trees derived from localities in Colorado, Utah, Arizona, and New Mexico that have more severe climates. Hereditary growth tendencies were less marked in the one progeny derived from a region having a climate considerably milder than that of the experimental area.

Characteristics as to persistence of needles were found not to be hereditary.

A study conducted cooperatively with the University of Montana revealed strong evidence that characteristics of internal structure of needles were inherited.

The present findings, revealing the existence of racial strains in ponderosa pine varying in rate of growth and hardiness, indicate that a tree's growth rate and hardiness should be investigated critically and the climatic characteristics of the locality in which it is

growing compared with those of the proposed planting site before the seed is used for reforestation. They indicate tentatively that the most suitable general territory in which to collect ponderosa pine seed for planting in northern Idaho is that extending from the Colville locality, in Washington, eastward a little beyond the Continental Divide and from the Salmon River to the Canadian boundary.

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